

### Chapter III

#### THE STRUGGLE FOR EXISTENCE FROM THE POINT OF VIEW OF THE MATHEMATICIANS

(1) In this chapter we shall make the acquaintance of the astonishing theories of the struggle for existence developed by mathematicians at a time when biologists were still far from any investigation of these phenomena and had but just begun to make observations in the field.

The first attempt at a quantitative study of the struggle for existence was made by Sir Ronald Ross ('08, '11). He undertook a theoretical investigation of the propagation of malaria, and came to conclusions which are of great interest for quantitative epidemiology and at the same time constitute an important advance in the understanding of the struggle for existence in general. Let us examine the fundamental idea of Ross. Our object will be to give an analysis of the propagation of malaria in a certain locality under somewhat simplified conditions. We assume that both emigration and immigration are negligible, and that in the time interval we are studying there is no increase of population or in other words the birth rate is compensated by the death rate. In such a locality a healthy person can be infected with malaria, according to Ross, if all the following conditions are realized: (1) That a person whose blood contains a sufficient number of gametocytes (sexual forms) is living in or near the locality. (2) That an Anopheline capable of carrying the parasites sucks enough of that person's blood. (3) That this Anopheline lives for a week or more afterwards under suitable conditions long enough to allow the parasites to mature within it, and (4) that it next succeeds in biting another person who is not immune to the disease or is not protected by quinine. The propagation of malaria in such a locality is determined in its general features by two continuous and 5 simultaneous processes: on the one hand, the number of new infections among people depends on the number and infectivity of the mosquitoes, and at the same time the infectivity of the mosquitoes is connected with the number of people in the given locality and the frequency of the sickness among them. Ross has expressed in mathematical terms this uninterrupted and simultaneous dependence of the infection of the first component on the second, and that of the second on the first, with the aid of what is called in mathematics simultaneous differential equations. These equations are very simple and we shall examine them at once. In a quite general form they can be represented as follows:

$$\left. \begin{aligned} \left\{ \begin{array}{l} \text{Rate of increase of} \\ \text{affected individuals} \\ \text{among the human} \\ \text{populations} \end{array} \right\} &= \left\{ \begin{array}{l} \text{New infections} \\ \text{per unit of time.} \\ \text{Depends on in-} \\ \text{fected mosqui-} \\ \text{toes} \end{array} \right\} - \left\{ \begin{array}{l} \text{Recoveries per unit} \\ \text{of time} \end{array} \right\} \\ \left\{ \begin{array}{l} \text{Rate of increase of} \\ \text{infected individuals} \\ \text{among the mosquito} \\ \text{population} \end{array} \right\} &= \left\{ \begin{array}{l} \text{New infections} \\ \text{per unit of time.} \\ \text{Depends on the} \\ \text{infected humans} \end{array} \right\} - \left\{ \begin{array}{l} \text{Deaths of infected} \\ \text{mosquitoes per unit} \\ \text{of time} \end{array} \right\} \end{aligned} \right\}$$

(2) Translating these relations into mathematical language we shall obtain the simultaneous differential equations of Ross. Let us introduce the following notation (that of Lotka (51)):

$$\left\{ \begin{array}{l} p = \text{total number of human individuals in a given locality.} \\ p^1 = \text{total number of mosquitoes in a given locality.} \end{array} \right.$$

$z$  = total number of people infected with malaria.  
 $z^1$  = total number of mosquitoes containing malaria parasites.

$$\left\{ \begin{array}{l} fz = \text{total number of infective malarials (number of persons with} \\ \text{gametocytes in the blood; a certain fraction of the total number of} \\ \text{malarials).} \\ f^1z^1 = \text{total number of infective mosquitoes (with matured parasites; a} \\ \text{certain fraction of the total number of mosquitoes containing parasites).} \end{array} \right.$$

$r$  = recovery rate, i.e., fraction of infected population that reverts to noninfected (healthy) state per unit of time.  
 $M^1$  = mosquito mortality, i.e., death rate per head per unit of time.  
 $t$  = time.

If a single mosquito bites a human being on an average  $b^1$  times per unit of time, then the  $f^1z^1$  infective mosquitoes will place  $b^1f^1z^1$  infective bites on human beings per unit of time. If the number of people not infected with malaria is  $(p-z)$ , then taken in a relative form as  $\frac{p-z}{p}$

it will show the relative number of healthy people in the total number of individuals of a given locality. Therefore, out of a total number of infective bites, equal per unit of time to  $b^1f^1z^1$ , a definite fraction equal to  $\frac{p-z}{p}$  falls to the lot of healthy people, and the number of infective

bites of healthy people per unit of time will be equal to:

$$b^1 f^1 z^1 \frac{p^1 - z^1}{p} \dots\dots\dots(2)$$

If every infective bite upon a healthy person leads to sickness, then the expression (2) will show directly the number of new infections per unit of time, which we can put in the second place of the first line of the equations (1). By analogous reasoning it follows that if every person is bitten on an average  $b$  times per unit of time, the total number of

infective people  $fz$  will be bitten  $bfz$  times, and a fraction  $\frac{p_1 - z_1}{p_1}$  of

these bites will be made by healthy mosquitoes which will thus become infected. Consequently the number of new infections among mosquitoes per unit of time will be:

$$bfz \frac{p^1 - z^1}{p^1} \dots\dots\dots(3)$$

Now, evidently, the total number of mosquito bites on human beings per unit of time will constitute a certain fixed value, which can be written either as  $b^1 p^1$ , i.e., the product of the number of mosquitoes by the number of bites made by each mosquito per unit of time, or as  $bp$ , i.e., the number of persons multiplied by the number of times each human being has been bitten. We have therefore  $bp = b^1 p^1$ , and finally

$$b = \frac{b^1 - p^1}{p} \dots\dots\dots(4)$$

Inserting the expression (4) into the formula (3) we obtain:

$$\frac{b^1 p^1 f z}{p p^1} (p^1 - z^1) = \frac{b^1 f z}{p} (p^1 - z^1) \dots\dots\dots(5)$$

The expression (5) fills the second place in the lower line in Ross's differential equations of malaria (1). It gives the number of new infections of mosquitoes per unit of time. We can now put down the rate of increase of infected individuals among the human population as

$\frac{dz}{dt}$  and the rate of increase in the number of infected mosquitoes as

$\frac{dz^1}{dt}$ . The number of recoveries per unit of time among human

individuals will be  $rz$ , as  $z$  represents the number of people infected

and  $r$  the rate of recovery, i.e., the fraction of the infected population recovering per unit of time. The number of infected mosquitoes dying per unit of time can be put down as  $M^1 z^1$ , since  $z^1$  denotes the number of mosquitoes infected, and  $M^1$  the death rate in mosquitoes per head per unit of time. We can now express the equation of Ross in mathematical symbols instead of words:

$$\left. \begin{aligned} \frac{dz}{dt} &= b^1 f^1 z^1 \frac{P - z}{P} - rz \\ \frac{dz^1}{dt} &= b^1 f z \frac{P^1 - z^1}{P} - M^1 z^1 \end{aligned} \right\} \dots\dots\dots(6)$$

These simultaneous differential equations of the struggle for existence express in a very simple and clear form the continuous dependence of the infection of people on the infectivity of the mosquitoes and vice versa. The increase in the number of sick persons is connected with the number of bites made by infective mosquitoes on healthy persons per unit of time, and at the same moment the increase in the number of infected mosquitoes depends upon the bites made by healthy mosquitoes on sick people. The equations (6) enable us to investigate the change with time ( $t$ ) of the number of person infected with malaria ( $z$ ).

The equations of Ross were submitted to a detailed analysis by Lotka ('23, '25) who in his interesting book *Elements of Physical Biology* gave examples of some other analogous equations. As Lotka remarks, a close agreement of the Ross equations with reality is not to be expected, as this equation deals with a rather idealized case: that of a constant population both of human beings and mosquitoes. "There is room here for further analysis along more realistic lines. It must be admitted that this may lead to considerable mathematical difficulties" (Lotka ('25, p. 83)).

(3) The equations of Ross point to the important fact that a mathematical formulation of the struggle for existence is a natural consequence of simple reasoning about this process, and that it is organically connected with it. The conditions here are more favorable than in other fields of experimental biology. In fact if we are engaged in a study of the influence of temperature or toxic substances on the life processes, or if we are carrying on investigations on the ionic theory of excitation, the quantitative method enables us to establish in most cases only purely empirical relations and the elaboration of a rational quantitative theory presents considerable difficulties owing to

the great complexity of the material. Often we cannot isolate certain factors as we should like, and we are constantly compelled to take into account the existence of complicated and insufficiently known systems. This produces the well known difficulties in applying mathematics to the problems of general physiology if we wish to go further than to establish purely empirical relations. As far as the rational mathematical theory of the struggle for existence is concerned, the situation is more favorable, because we can analyze the properties of our species grown separately in laboratory conditions, then make various combinations and in this way can formulate correctly the corresponding theoretical equations of the struggle for life.

(4) Besides the interest of the equations of Ross as the first attempt to formulate mathematically the struggle for existence, they allow us to answer a very common objection of biologists to such equations in general. It is frequently pointed out that there is no sense in searching for exact equations of competition as this process is very inconstant, and as the slightest change in the environmental conditions or in the quantities of each species can lead to the result that instead of the second species supplanting the first it is the first species itself that begins to supplant the second. As Jennings ('33) points out, there exists a strong strain of uniformitarianism in many biologists. The idea that we can observe one effect, and then the opposite, seems to them a negation of science. In the spreading of malaria something analogous actually takes place. Ross came to the following interesting conclusion about this matter: (1) Whatever the original number of malaria cases in the locality may have been, the ultimate malaria ratio will tend to settle down to a fixed figure dependent on the number of Anophelines and the other factors—that is if these factors remain constant all the time. (2) If the number of Anophelines is sufficiently high, the ultimate malaria ratio will become fixed at some figure between 0 per cent and 100 per cent. If the number of Anophelines is low (say below 40 per person) the ultimate malaria rate will tend to zero—that is, the disease will tend to die out. All these relations Ross expressed quantitatively, and later they were worked out very elegantly by Lotka. This example shows that a change in the quantitative relations between the components can change entirely the course of the struggle for existence. Instead of an increase of the malaria infection and its approach to a certain fixed value, there may be a decrease reaching an equilibrium with a complete absence of malaria. In spite of all this there remains a certain invariable law of the struggle for existence which Ross's equations express. In this way we see what laws are to be sought in the investigation of the complex and unstable competition processes. The laws which exist here are not of the type the biologists are accustomed to deal with. These laws may be formulated in terms of certain equations of the struggle for existence. The parameters in these equations easily undergo various changes and as a result a whole

range of exceedingly dissimilar processes arises.

## II

(1) The material just presented enables one to form a certain idea as to what constitutes the essence of the mathematical theories of the struggle for existence. In these theories we start by formulating then dependence of one competitor on another in a verbal form, then translate this formulation into mathematical language and obtain differential equations of the struggle for existence, which enable us to draw definite conclusions about the course and the results of competition. Therefore all the value of the ulterior deductions depends on the question whether certain fundamental premises have been correctly formulated. Consequently before proceeding any further to consider more complicated mathematical equations of the struggle for existence we must with the greatest attention, relying upon the experimental data already accumulated, decide the following question: what are the premises we have a right to introduce into our differential equations? As the problem of the struggle for existence is a question of the growth of mixed populations and of the replacement of some components by others, we ought at once to examine this problem: what is exactly known about the multiplication of animals and the growth of their homogeneous populations?

Of late years among ecologists the idea has become very wide spread that the growth of homogeneous populations is a result of the interaction of two groups of factors: the biotic potential of the species and the environmental resistance [Chapman '28, '31]. The biotic potential<sup>1</sup> represents the potential rate of increase of the species under given condition. It is realized if there are no restrictions of food, no toxic waste products, etc. Environmental resistance can be measured by the difference between the potential number of organisms which can appear during a fixed time in consequence of the potential rate of increase, and the actual number of organisms observed in a given microcosm at a determined time. Environmental resistance is thus expressed in terms of reduction of some potential rate of increase, characteristic for the given organisms under given conditions. This idea is a correct one and it clearly indicates the essential factors which are operating in the growth of a homogeneous population of organisms.

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<sup>1</sup>What Chapman calls a "partial potential."

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However, as yet among ecologists the ideas of biotic potential and of

environmental resistance are not connected with any quantitative conceptions. Nevertheless Chapman in his interesting book *Animal Ecology* arrives at the conclusion that any further progress here can only be achieved on a quantitative basis, and that in future "this direction will probably be one of the most important fields of biological science, which will be highly theoretical, highly quantitative, and highly practical.

(2) There is no need to search for a quantitative expression of the potential rate of increase and of the environmental resistance, as this problem had already been solved by Verhulst in 1838 and quite independently by Raymond Pearl and Reed in 1920. However, ecologists did not connect their idea of biotic potential with these classical works. The logistic curve, discovered by Verhulst and Pearl, expresses quantitatively the idea that the growth of a population of organisms is at every moment of time determined by the relation between the potential rate of increase and "environmental resistance." The rate of multiplication or the increase of the number of organisms

( $N$ ) per unit of time ( $t$ ) can be expressed as  $\frac{dN}{dt}$ . The rate of

multiplication depends first on the potential rate of multiplication of each organism ( $b$ ), i.e., on the potential number of offspring which the organism can produce per unit of time. The total potential number of offspring that can be produced by all the organisms per unit of time can be expressed as the product of the number of organisms ( $N$ ) and the potential increase ( $b$ ) from each one of them, i.e.,  $bN$ . Therefore the potential increase of the population in a certain infinitesimal unit of time will be expressed thus:

$$\frac{dN}{dt} = bN \dots\dots\dots(7)$$

This expression represents a differential equation of the population growth which would exist if all the offspring potentially possible were produced and actually living. It is an equation of geometric increase, as at every given moment the rate of growth is equal to the number of organisms ( $N$ ) multiplied by a certain constant ( $b$ ).

As has been already stated, the potential geometrical rate of population growth is not realized, and its reduction is due to the environmental resistance. This idea was quantitatively expressed by Pearl in such a form that the potential geometric increase at every moment of time is only partially realized, depending on how near the already accumulated size of the population ( $N$ ) approaches the maximal population ( $K$ ) that can exist in the given microcosm with the given level of food resources, etc. The difference between the maximally

possible and the already accumulated population ( $K-N$ ), taken in a relative form, i.e., divided by the maximal population  $\left(\frac{K-N}{K}\right)$ , shows the relative number of the "still vacant places" for definite species in a given microcosm at a definite moment of time. According to the number of the still vacant places only a definite part of the potential rate of increase can be realized. At the beginning of the population growth when the relative number of unoccupied places is considerable the potential increase is realized to a great extent, but when the already accumulated population approaches the maximally possible or saturating one, only an insignificant part of the biotic potential will be realized (Fig. 3). Multiplying the biotic potential of the population ( $bN$ ) by the relative number of still vacant places or its "degree of realization"  $\frac{K-N}{K}$  we shall have the increase of population per infinitesimal unit of time:

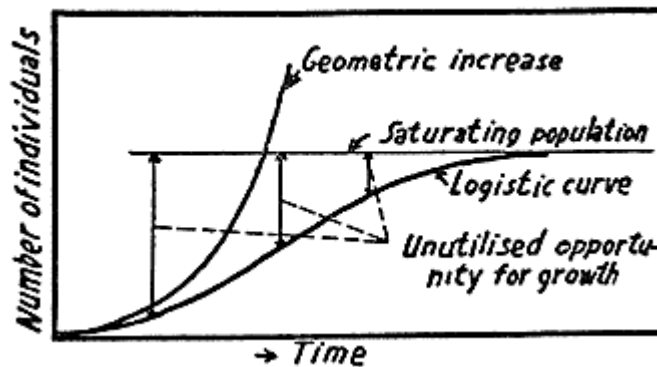


Fig. 3. The curve of geometric increase and the logistic curve

$$\left\{ \begin{array}{l} \text{Rate of growth} \\ \text{or increase per} \\ \text{unit of time} \end{array} \right\} = \left\{ \begin{array}{l} \text{Potential increase} \\ \text{of population per} \\ \text{unit of time} \end{array} \right\} \times \left\{ \begin{array}{l} \text{Degree of realization} \\ \text{of the potential increase.} \\ \text{Depends on the number} \\ \text{of still vacant places.} \end{array} \right\} \dots\dots(8)$$

Expressing this mathematically we have:

$$\frac{dN}{dt} = bn \frac{K - N}{K} \dots\dots\dots(9)$$

This is the differential equation of the Verhulst-Pearl logistic curve.<sup>2</sup>



<sup>2</sup> It is to be noted that we have to do in all the cases with numbers of individuals per unit of volume or area, e.g., with population *densities* ( $N$ ).

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(3) Before going further we shall examine the differential form of the logistic curve in a numerical example. Let us turn our attention to the growth of a number of individuals of an infusorian, *Paramecium caudatum*, in a small test tube containing  $0.5 \text{ cm}^3$  of nutritive medium (with the sediment; see Chapter V). The technique of experimentation will be described in detail further on. Five individuals of *Paramecium* (from a pure culture) were placed in such a microcosm, and for six days the number of individuals in every tube was counted daily. The average data of 63 separate counts are given in Figure 4. This figure shows that the number of individuals in the tube increases, rapidly at first and then more slowly, until towards the fourth day it attains a certain maximal level saturating the given microcosm. The character of the curve should be the same if we took only one mother cell at the start. Indeed, if one *Paramecium* is isolated and its products segregated as a *pure culture*, the generation time of each cell is not identically the same as that of its neighbors, and consequently at any given moment some cells are dividing, whereas the others are at various intermediate stages of their reproductive cycle; it is, however, no longer possible to divide the population up into permanent categories, since a *Paramecium* which divides rapidly tends to give rise to daughter cells which divide slowly, and vice versa. The rate of increase of such a population will be determined by the percentage of cells actually dividing at any instant, and the actual growth of the population can be plotted as a smooth curve, instead of a series of points restricted to the end of each reproductive period. The smooth curve of Figure 4 is drawn according to the equation of the logistic curve, and its close coincidence with the results of the observations shows that the logistic curve represents a good empirical description of the growth of the population. The practical method of fitting such an empirical curve will also be considered further (Appendix II). The question that interests us just now is this: what is, according to the logistic curve, the potential rate of increase of under our conditions, and how does it become reduced in the process of growth as the environmental resistance increases?

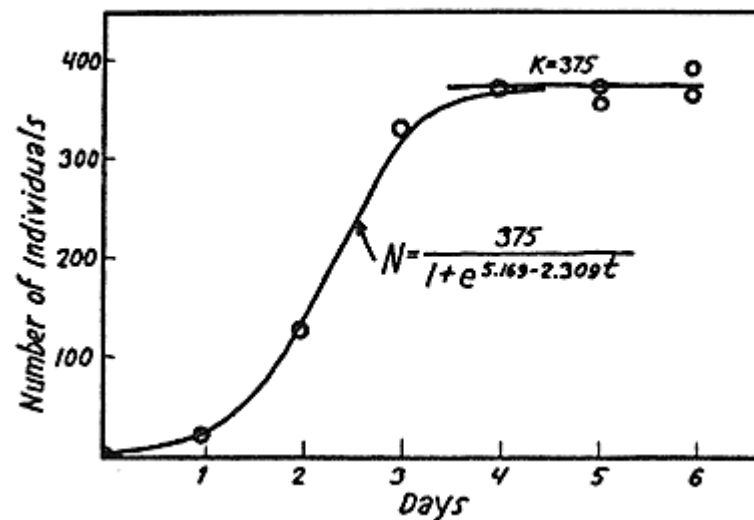


Fig. 4. The growth of population of *Paramecium caudatum*

According to Figure 4, the maximal possible number of *Paramecia* in a microcosm of our type, or the saturating population,  $K = 375$  individuals. As a result of the very simple operation of fitting the logistic curve to the empirical observations, the coefficient of multiplication or the biotic potential of one *Paramecium* ( $b$ ) was found. It is equal to 2.309. This means that per unit of time (one day) under our conditions of cultivation every *Paramecium* can potentially give 2.309 new *Paramecia*. It is understood that the coefficient  $b$  is taken from a differential equation and therefore its value automatically obtained for a time interval equal to one day is extrapolated from a consideration of infinitesimal sections of time. This value would be realized if the conditions of an unoccupied microcosm, i.e., the absence of environmental resistance existing only at the initial moment of time, existed during the entire 24 hours. It is automatically taken into account here that if at the initial moment the population increases by a certain infinitesimal quantity proportional to this population, at the next moment the population plus the increment will increase again by a certain infinitesimal quantity proportional no longer to the initial population, but to that of the preceding moment. The coefficient  $b$  represents the rate of increase in the absence of environmental resistance under certain fixed conditions. At another temperature and under other conditions of cultivation the value  $b$  will be different. Table IV gives the constants of growth of the population of *Paramecia* calculated on the basis of the logistic curve. There is shown  $N$  or the number of *Paramecia* on the first, second, third and fourth days of growth. These numbers represent the ordinates of the logistic curve which passes near the empirical observations and smoothes certain insignificant denations. The values  $bN$  given in Table IV express the potential rate of increase of the whole population at different moments of growth, or the number of offspring which a given population of

Paramecia can potentially produce within 24 hours at these moments. We must repeat here what has been already said in calculating the value  $b$ . The potential rate  $bN$  exists only within an infinitesimal time and should these conditions exist during 24 hours the values shown in Table IV would be obtained. The expression  $\frac{K - N}{K}$  shows the relative number of yet unoccupied places. At the beginning of the population growth when  $N$  is very small the value  $\frac{K - N}{K}$  approaches unity. In other words the potential rate of growth is almost completely realized. As the population grows,  $\frac{K - N}{K}$  approaches zero. The environmental resistance can be measured by that part of the potential increase which has not been realized—the greater the resistance the larger the unrealized part. This value can be obtained by subtracting  $\frac{K - N}{K}$  from unity. At the beginning of growth the environmental resistance is small and  $1 - \frac{K - N}{K}$  approaches zero. As the population increases the environmental resistance increases also and  $1 - \frac{K - N}{K}$  approaches unity. This means that the potential increase remains almost entirely unrealized. Multiplying  $bN$  by  $\frac{K - N}{K}$  for a given moment we obtain a rate of population growth  $\frac{dN}{dt}$ , which increases at first and then decreases. The corresponding numerical data are given in Table IV and Figure 5.

TABLE IV  
*The growth of population of Paramecium caudatum*  
*b*(coefficient of multiplication; potential progeny per individual per day) = 2.309.  
*K* (maximal population) = 375.

	TIME IN DAYS			
	1	2	3	4
N (number of individuals according to the logistic curve).	20.4	137.2	319.0	3 69.0

$bN$ (potential increase of the population per day)	47.1	316.8	736.6	852.0
$\frac{K - N}{K}$ (degree of realization of the potential increase)	0.945	0.633	0.149	0.016
$1 - \frac{K - N}{K}$ (environmental resistance)	0.055	0.367	0.851	0.984
$\frac{dN}{dt} bN \frac{K - N}{K}$ (rate of growth of the population)	44.5	200.0	109.7	13.6
$\frac{bN - \frac{dN}{dt}}{\frac{dN}{dt}}$ (intensity of the struggle for existence)	0.058	0.584	5.72	61.7

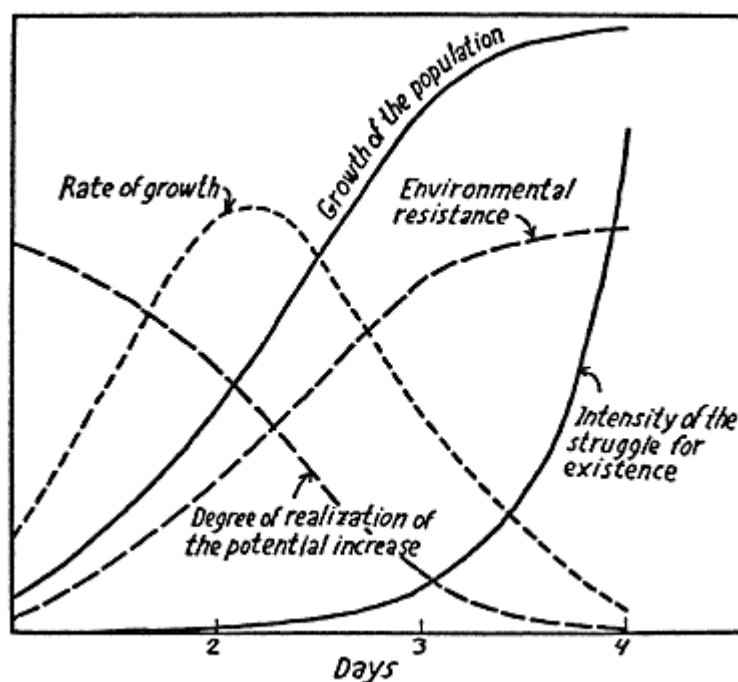


Fig. 5. The characteristics of competition in a homogeneous population of *Paramecium caudatum*

(4) We must now analyze a very important principle which was clearly understood by Darwin, but which is still waiting for its rational

quantitative expression. I mean *the intensity of the struggle for existence* between individuals of a given group.<sup>3</sup> *The intensity of the struggle for existence is measured by the resistance which must be overcome in order to increase the number of individuals by a unit at a given moment of time.* As we measure the environmental resistance by the eliminated part of the potential increase, our idea can be formulated thus: what amount of the eliminated fraction of the potential increase falls upon a unit of the realized part of the increase at a given moment of time? The intensity of the struggle for existence keeps constant only for an infinitesimal time and its value shows with what losses of the potentially possible increment the establishment of a new unit in the population is connected. The realized value of increase at a given moment is equal to

$$\frac{dN}{dt} = bN \frac{K - N}{K}$$

and the unrealized one:

$$bN \left( 1 - \frac{K - N}{K} \right) = bN - bN \frac{K - N}{K} = bN - \frac{dN}{dt}$$

Then the amount of unrealized potential increase per unit of realized increase, or the intensity of the struggle for existence (*i*), will be expressed thus:

$$i = \frac{\text{unrealized part of the potential increase}}{\text{realized part of the potential increase}} = \frac{bN - \frac{dN}{dt}}{\frac{dN}{dt}} \dots\dots\dots(10)$$

The values of *i* for a population of Paramecia are given in Table IV and we see that at the beginning of the population growth the intensity of the struggle for existence is not great, but that afterwards it increases considerably. Thus on the first day there are 0.058 "unrealized" Paramecia for every one realized, but on the fourth day 61.7 "unrealized" ones are lost for one realized (Fig. 6). Figure 5 shows graphically the changes of all the discussed characteristics in the course of the population growth of Paramecia.

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<sup>3</sup> As we have seen in Chapter II, botanists are beginning to deal with the intensity of the struggle for existence, simply characterizing it by the per cent of destroyed individuals. Haldane

investigating the connection of the intensity of selection ('31) and in his interesting book *The Causes of Evolution* ('32) specifies the intensity of competition by Z and determines it as the proportion of the number of eliminated individuals to that of the surviving ones. Thus if the mortality is equal to 9 per cent,  $Z=9/91$ , i.e., approximately 0.1.

(5) The intensity of the struggle for existence can evidently be expressed in this form only in case the population grows, i.e., if the number of individuals increases continually. If growth ceases the population is in a state of equilibrium, and the rate of growth  $\frac{dN}{dt} = 0$ ;

in this case the expression of intensity will take another form. Population in a state of equilibrium represents a stream moving with a certain rapidity: per unit of time a definite number of individuals perishes, and new ones take their places. The number of these liberated places is not large if compared with the number of organisms that the population can produce in the same unit of time according to the potential coefficients of multiplication. Therefore a considerable part of the potentially possible increase of the population will not be realized and liberated places will be occupied only by a very small fraction of it. If the potential increase of a population in the state of equilibrium per infinitesimal unit of time is  $\eta$ , and a certain part (h) of this increase takes up the liberated places, it is evident that a part (1- h) will remain unrealized. The mechanism of this "nonrealization" is of course different in different animals. Then as before the intensity of the struggle for existence, or the proportion of the unrealized part of the potential increase to the realized part, will be:

$$i = \frac{(1 - \eta)b_1N_1}{\eta b_1N_1} = \frac{1 - \eta}{\eta} \dots\dots\dots(10')$$

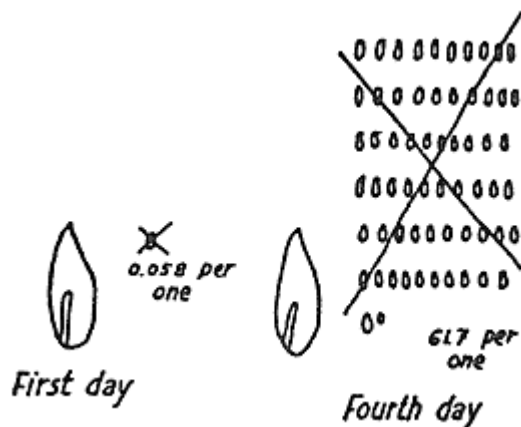


Fig. 6. Intensity of the struggle for existence in *Paramecium caudatum*. On the first day of the growth of the population 0.058 "unrealized" Paramecia are lost per one realized, but on the fourth day

61.7 per one.

(6) We may say that the Verhulst-Pearl logistic curve expresses quantitatively and very simply the struggle for existence which takes place between individuals of a homogeneous group. Further on we shall see how complicated the matter becomes when there is competition between individuals belonging to two different species. But one must not suppose that an intragroup competition is a very simple thing even among unicellular organisms. Though in the majority of cases the symmetrical logistic curve with which we are now concerned expresses satisfactorily the growth of a homogeneous population, certain complicating factors often appear and for some species the curves are asymmetrical, i.e., their concave and convex parts are not similar. Though this does not alter our reasoning, we have to take into account a greater number of variables which complicate the situation. Here we agree completely with the Russian biophysicist P. P. Lasareff ('23) who has expressed on this subject, but in connection with other problems, the following words: "For the development of a theory it is particularly advantageous if experimental methods and observations do not at once furnish data possessing a great degree of accuracy and in this way enable us to ignore a number of secondary accompanying phenomena which make difficult the establishment of simple quantitative laws. In this respect, e.g., the observations of Tycho Brahe which gave to Kepler the materials for formulating his laws, were in their precision just sufficient to characterize the movement of the planets round the sun to a first approximation. If on the contrary Kepler had had at his disposal the highly precise observations which we have at present, then certainly his attempt to find an empirical law owing to the complexity of the whole phenomenon could not have led him to simple and sufficiently clear results, and would not have given to Newton the material out of which the theory of universal gravitation has been elaborated.

"The position of sciences in which the methods of experimentation and the theory develop hand in hand is thus more favorable than the position of those fields of knowledge where experimental methods far outstrip the theory, as is, e.g., observed in certain domains of experimental biology, and then the development of the theory becomes more difficult and complicated" (p. 6).

Therefore we must not be afraid of the simplicity of the logistic curve for the population of unicellular organisms and criticize it from this point of view. At the present stage of our knowledge it is just sufficient for the rational construction of a theory of the struggle for existence, and the secondary accompanying circumstances investigators will discover in their later work.<sup>4</sup>

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<sup>4</sup>The usual objection to the differential logistic equation is that it is too simple and does not reflect all the "complexity" of growth of a population of lower organisms. In Chapter V we shall see that this remark is to a certain extent true for some populations of Protozoa. The realization of the biotic potential in certain cases actually does not *gradually diminish* with the decrease in the unutilized opportunity for growth. But this ought not to frighten any one acquainted with the methodology of modern physics: it is evident that the expression is but a first approximation to what actually exists, and, if necessary, it can be easily generalized by introducing before  $1/V$  a certain coefficient, which would change with the growth of the culture (for further discussion see Chapter V).

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(7) The application of quantitative methods to experimental biology presents such difficulties, and has more than once led to such erroneous results that the reader would have the right to consider very sceptically the material of this chapter. It is very well known that the differential equations derived from the curves observed in an experiment can be only regarded as empirical expressions and they do not throw any real light on the underlying factors which control the growth of the population. The only right way to go about the investigation is, as Professor Gray ('29) says, a direct study of factors which control the growth rate of the population and the expression of these factors in a quantitative form. In this way real differential equations will be obtained and in their integrated form they will harmonize with the results obtained by observation. In our experimental work described in the next chapter special attention has been given to a direct study of the factors controlling growth in the simplest populations of yeast cells. It has become evident that *the value of the environmental resistance which we have determined on the basis of a purely physiological investigation coincides completely with the value of the environmental resistance calculated according to the logistic equation*, using the latter as an empirical expression of growth. In this way we have proved that the logistic equation actually expresses the mechanism of the growth of the number of unicellular organisms within a limited microcosm. All this will be described in detail in the next chapter.

### III

(1) We are now sufficiently prepared for the acquaintance with the mathematical equations of the struggle for existence, and for a critical consideration of the premises implied in them. Let us consider first of all the case of competition between two species for the possession of a common place in the microcosm. This case was considered theoretically for the first time by Vito Volterra in 1926. An experimental investigation of this case was made by Gause ('32b), and at the same time Lotka ('32b) submitted it to a further analysis along theoretical lines. If there is competition between



two species for a common place in a limited microcosm, we can quite naturally extend the premises implied in the logistic equation. The rate of growth of each of the competing species in a mixed population will depend on (1) the potential rate of population increase of a given species ( $b_1N_1$  or  $b_2N_2$ ) and (2) on the unutilized opportunity for growth of this species, just as in the case of a population of the first and second species growing separately. But unutilized opportunity for growth of a given species in a mixed population is a complex variable. It measures the number of places which are still vacant for the given species in spite of the presence of another species, which is consuming the common food, excreting waste products and thereby depriving the first one of some of the places. Let us denote as before by  $N_1$  the number of individuals of the first species, though, as we shall see further on, we shall have to deal in many cases not with the numbers of individuals but with masses of species (= the weight of the organisms present or its equivalent) and we shall introduce corresponding alterations. The unutilized opportunity for growth, or the degree of realization of the potential increase for the first species in a mixed

population, may be expressed thus:  $\frac{K_1 - (N_1 + m)}{K_1}$ , where  $K_1$  is the

maximal possible number of individuals of this species when grown separately under given conditions,  $N_1$  is the already accumulated number of individuals of the first species at a given moment in the mixed population, and  $m$  is the number of the places of the first species in terms of the number of individuals of this species, which are taken up by the second species at a given moment. The unutilized opportunity for growth of the first species in the mixed population can be better understood if we compare it with the value of the unutilized opportunity for the separate growth of the same species. In the latter case the unutilized opportunity for growth is expressed by the difference (expressed in a relative form) between the maximal number of places and the number of places already occupied by the given species. Instead of this for the mixed population we write the difference between the maximal number of places and that of the places already taken up by our species together with the second species growing simultaneously.

(2) An attempt may be made to express the value  $m$  directly by the number of individuals of the second species at a given moment, which can be measured in the experiment. But it is of course unlikely that in nature two species would utilize their environment in an absolutely identical way, or in other words that equal numbers of individuals would consume (on an average) equal quantities of food and excrete equal quantities of metabolic products of the same chemical composition. Even if such cases do exist, as a rule different species do not utilize the environment in the same way. Therefore the number of individuals of the second species accumulated at a given moment of time in a mixed population in respect to the place it occupies, which might be suitable for the first species, is by no means

equivalent to the same number of individuals of the first species. The individuals of the second species have taken up a certain larger or smaller place. If  $N_2$  expresses the number of individuals of the second species in a mixed population at a given moment, than the places of the first species which they occupy *in terms of the number of individuals of the first species*, will be  $m = a N_2$ . Thus, the coefficient  $a$  is the coefficient reducing the number of the individuals of the second species to the number of places of the first species which they occupy. This coefficient  $a$  shows the degree of influence of one species upon the unutilized opportunity for growth of another. In fact, if the interests of the different species do not clash and if the microcosm they occupy places of a different type or different "niches" then the degree of influence of one species on the opportunity for growth of another, or the coefficient  $a$ , will be equal to zero. But if the species lay claim to the very same "niche," and are more or less equivalent as concerns the utilization of the medium, then the coefficient  $a$  will approach unity. And finally if one of the species utilizes the environment very unproductively, i.e., if each individual consumes a great amount of food or excretes a great quantity of waste products, then it follows that an individual of this species occupies as large a place in the microcosm as would permit another species to produce many individuals, and the coefficient  $a$  will be large. In other words an individual of this species will occupy the place of many individuals of the other species. If we remember here the specificity of the metabolic products, and all the very complex relations which can exist between the species, we shall understand how useful we may find the coefficient of the struggle for existence  $a$ , which objectively shows how many places suitable for the first species are occupied by one individual of the second.

Taking the coefficient  $a$ , we can now express in the following manner the unutilized opportunity for growth of the first species in a mixed population:

$\frac{K_1 - (N_1 + aN_2)}{K_1}$ . The unutilized opportunity for growth of the second

species in a mixed population will have a similar expression:

$\frac{K_2 - (N_2 + bN_1)}{K_2}$ . The coefficient of the struggle for existence  $b$

indicates the degree of influence of every individual of the first species on the number of places suitable for the life of the second species. These two expressions enable one to judge in what degree the potential increase of each species is realized in a mixed population.

(3) As we have already mentioned in analyzing the Ross equations, an important feature of mixed populations is the simultaneous influence upon each other of the species constituting them. The rate of growth of the first species depends upon the number of places already occupied by it as well as by the second species at a given moment.

As growth proceeds the first species increases the number of places already occupied, and thus affects the growth of the second species as well as its own. We can introduce the following notation:

$\frac{dN_1}{dt}, \frac{dN_2}{dt}$  = rates of growth of the number of individuals of the first and second species in a mixed population at a given moment.

$N_1, N_2$  = number of individuals of the first and second species in a mixed population at a given moment.

$b_1, b_2$  = potential coefficients of increase in the number of individuals of the first and second species.

$K_1, K_2$  = maximal numbers of individuals of the first and second species under the given conditions when separately grown.

$a, b$  = coefficients of the struggle for existence.

The rate of growth of the number of individuals of the first species in a mixed population is proportional to its potential rate ( $b_1N_1$ ), which in every infinitesimal time interval is realized in greater or less degree depending on the relative number of the still vacant places:  $\frac{K_1 - (N_1 + aN_2)}{K_1}$ . An

analogous relationship holds true for the second species. The growth of the first and second species is simultaneous. It can be expressed by the following system of simultaneous differential equations:

$$\left\{ \begin{array}{l} \text{Rate of growth} \\ \text{of the first species} \\ \text{in a mixed population} \end{array} \right\} = \left\{ \begin{array}{l} \text{Potential increase} \\ \text{of the population} \\ \text{of the first species} \end{array} \right\} \times \left\{ \begin{array}{l} \text{Degree of realization} \\ \text{of the potential increase.} \\ \text{Depends on the number} \\ \text{of still vacant places.} \end{array} \right\}$$

$$\left\{ \begin{array}{l} \text{Rate of growth of the} \\ \text{second species in a} \\ \text{mixed population} \end{array} \right\} = \left\{ \begin{array}{l} \text{Potential increase} \\ \text{of the population of} \\ \text{the second species} \end{array} \right\} \times \left\{ \begin{array}{l} \text{Degree of realization of} \\ \text{the potential increase.} \\ \text{Depends on the number} \\ \text{of still vacant places.} \end{array} \right\}$$

..(11)

Translating this into mathematical language we have:

$$\left. \begin{aligned} \frac{dN_1}{dt} &= b_1 N_1 \frac{K_1 - (N_1 + \alpha N_2)}{K_1} \\ \frac{dN_2}{dt} &= b_2 N_2 \frac{K_2 - (N_2 + \beta N_1)}{K_2} \end{aligned} \right\} \dots\dots\dots(12)$$

The equation of the struggle for existence which we have written express quantitatively the process of competition between two species for the possession of a certain common place in the microcosm. They are founded on the idea that every species possesses a definite potential coefficient of multiplication but that the realization of these potentialities ( $b_1 N_1$  and  $b_2 N_2$ ) of two species is impeded by *four* processes hindering growth: (1) in increasing the first species diminishes its own opportunity for growth (accumulation of  $N_1$ ), (2) in increasing the second species decreases the opportunity for growth of the first species ( $\alpha N_2$ ), (3) in increasing the second species decreases its own opportunity for growth (accumulation of  $N_2$ ) and (4) the increase of the first species diminishes the opportunity for growth of the second species ( $\beta N_1$ ). Whether the first species will be victorious over the second, or whether it will be displaced by the second depends, first, on the properties of each of the species taken separately, i.e., on the potential coefficients of increase in the given conditions ( $b_1, b_2$ ) and on the maximal numbers of individuals ( $K_1, K_2$ ). But when two species enter into contact with one another, new coefficients of the struggle for existence  $\alpha$  and  $\beta$  begin to operate. They characterize the degree of influence of one species upon the growth of another, and participate in accordance with the equation (12) in producing this or that outcome of the competition.

(4) It is the place to note here that the equation (12) as it is written does not permit of any equilibrium between the competing species occupying the same "niche," and leads to the entire displacing of one of them by another. This has been pointed out by Volterra ('26), Lotka ('32b) and even earlier by Haldane ('24), and for the experimental confirmation and a further analysis of this problem the reader is referred to Chapter V. We can only remark here that this is immediately evident from the equation (12). The stationary state

occurs whenever  $\frac{dN_1}{dt}$  and  $\frac{dN_2}{dt}$  both vanish together

$$\left( \frac{dN_1}{dt} = \frac{dN_2}{dt} = 0 \right),$$

and the mathematical considerations show that with usual  $\alpha$  and  $\beta$  there cannot simultaneously exist positive values for both  $N_1$  and  $N_2$ . One of the species must eventually disappear. This apparently harmonizes with the biological observations. As we have pointed out in Chapter II, both species survive indefinitely only when they occupy

different niches in the microcosm in which they have an advantage over their competitors. Experimental investigations of such complicated systems are in progress at the time of this writing.

(5) We have just discussed a very important set of equations of the competition of two species for a common place in the microcosm, and it remains to make in this connection a few historical remarks. Analogous equations dealing with a more special case of competition between two species for a common food were for the first time given in 1926 by the Italian mathematician Vito Volterra who was not acquainted with the investigations of Ross and of Pearl.

Volterra assumed that the increase in the number of individuals obeys the law of geometric increase:  $\frac{dN}{dt} = bN$ , but as the number of individuals ( $N$ ) accumulates, the coefficient of increase ( $b$ ) diminishes to a first approximation proportionally to this accumulation ( $b-l N$ ), where  $l$  is the coefficient of proportionality. Thus we obtain:

$$\frac{dN}{dt} = (b - \lambda N)N \dots\dots\dots(13)$$

It can be easily shown, as Lotka ('32) remarks, that the equation of Volterra (13) coincides with the equation of the logistic curve of Verhulst-Pearl (9). In fact, if we call the rate of growth per individual a relative rate of growth and denote it as:  $\frac{1}{N} \frac{dN}{dt}$ , then the equation (13) will have the following form:

$$\frac{1}{N} \cdot \frac{dN}{dt} = b - \lambda N \dots\dots\dots(14)$$

This enables us to formulate the equation (13) in this manner: the relative rate of growth represents a linear function of the number of individuals  $N$ , as  $b-l N$  is the equation of a straight line. If we now take the equation of the Verhulst-Pearl logistic curve (9):  $\frac{dN}{dt} = bN \frac{K - N}{K}$  and make the following transformations:

$$\frac{dN}{dt} = bN \left( 1 - \frac{1}{K} N \right); \frac{1}{N} \cdot \frac{dN}{dt} = b \left( 1 - \frac{1}{K} N \right), \text{ we shall have}$$

$$\frac{1}{N} \cdot \frac{dN}{dt} = b - \frac{b}{K} N \dots\dots\dots(15)$$

In other words the logistic curve possesses the property that with an increase in the number of individuals the relative rate of growth decreases linearly (this has been recently mentioned by Virinsor ('32)). Consequently the expression (13) according to which we must subtract from the coefficient of increase  $b$  a certain value proportional to the accumulated number of individuals in order to obtain the rate of growth, and the expression (9), according to which we must multiply the geometric increase  $bN$  by a certain "degree of its realization," coincide with one another. Both are based on a broad mathematical assumption of a linear relation between the relative rate of growth and the number of individuals. Volterra extended the equation (13) to the competition of two species for common food, assuming that the presence of a certain number of individuals of the first species ( $N_1$ ) decreases the quantity of food by  $h_1N_1$ , and the presence of  $N_2$  individuals of the second species decreases the quantity of food by  $h_2N_2$ . Therefore, both species together decrease the quantity of food by  $h_1 N_1 + h_2N_2$ , and the coefficient of multiplication of the first species decreases in connection with the diminution of food:

$$b_1 - \lambda_1 (h_1 N_1 + h_2 N_2) \dots\dots\dots(16)$$

But for the second species the degree of influence of the decrease of food on the coefficient of multiplication  $b_2$  will be different (1 2), and we shall obtain:

$$b_2 - \lambda_2 (h_1 N_1 + h_2 N_2) \dots\dots\dots(17)$$

Starting from these expressions Volterra ('26) wrote the following simultaneous differential equations of the competition between two species for common food:

$$\left. \begin{aligned} \frac{dN_1}{dt} &= [b_1 - \lambda_1 (h_1 N_1 + h_2 N_2)] N_1 \\ \frac{dN_2}{dt} &= [b_2 - \lambda_2 (h_1 N_1 + h_2 N_2)] N_2 \end{aligned} \right\} \dots\dots\dots(18)$$

These equations represent, therefore, a natural extension of the principle of the logistic curve, and the equation (12) written by Gause ('32b) coincides with them. Indeed the equation (12) can be transformed in this manner:

$$\left. \begin{aligned} \frac{dN_1}{dt} &= b_1 N_1 \left[ 1 - \left( \frac{1}{K_1} N_1 + \frac{\alpha}{K_1} N_2 \right) \right] \\ \frac{dN_2}{dt} &= b_2 N_2 \left[ 1 - \left( \frac{1}{K_2} N_2 + \frac{\beta}{K_2} N_1 \right) \right] \end{aligned} \right\} \text{or}$$

$$\left. \begin{aligned} \frac{dN_1}{dt} &= b_1 N_1 \left[ 1 - \left( \frac{1}{K_1} N_1 + \frac{\alpha}{K_1} N_2 \right) \right] N_1 \\ \frac{dN_2}{dt} &= b_2 N_2 \left[ 1 - \left( \frac{1}{K_2} N_2 + \frac{\beta}{K_2} N_1 \right) \right] N_2 \end{aligned} \right\} \dots\dots\dots(19)$$

The result of the transformation shows that the equation (12) coincides with Volterra's equation (18), but it does not include any parameters dealing with the food consumption, and simply expresses the competition between species in terms of the growing populations themselves. As will be seen in the next chapter, the equation (12) is actually realized in the experiment.

#### IV

(1) In the present book our attention will be concentrated on an experimental study of the struggle for existence. In this connection we are interested only in those initial stages of mathematical researches which have already undergone an experimental verification. At the same time we are writing for biological readers and we would not encumber them by too numerous mathematical material. All this leads us to restrict ourselves to an examination of only a few fundamental equations of the struggle for existence, referring those who are interested in mathematical questions to the original investigations of Volterra, Lotka and others.

We shall now consider the second important set of equations of the struggle for existence, which deals with the destruction of one species by another. The idea of these equations is very near to those of Ross which we have already analyzed. They were given for the first time by Lotka ('20b) and independently by Volterra ('26). After the previous discussion these equations ought not to present any difficulties. Let us consider the process of the prey  $N_1$  being devoured by another species, the predator  $N_2$ . We can put it in a general form:

$$\left. \begin{aligned}
 \left\{ \begin{array}{l} \text{Change in the} \\ \text{number of prey} \\ \text{per unit of time} \end{array} \right\} &= \left\{ \begin{array}{l} \text{Natural increase} \\ \text{of prey per unit} \\ \text{of time} \end{array} \right\} - \left\{ \begin{array}{l} \text{Destruction of} \\ \text{the prey by the} \\ \text{predators per} \\ \text{unit of time} \end{array} \right\} \\
 \left\{ \begin{array}{l} \text{Change in the} \\ \text{number of pre-} \\ \text{dator per unit} \\ \text{of time} \end{array} \right\} &= \left\{ \begin{array}{l} \text{Increase in the} \\ \text{number of pre-} \\ \text{dators per unit} \\ \text{of time resulting} \\ \text{from the devou-} \\ \text{ring of the prey} \end{array} \right\} - \left\{ \begin{array}{l} \text{Deaths of the} \\ \text{predators per} \\ \text{unit of time} \end{array} \right\}
 \end{aligned} \right\} \dots\dots\dots(20)$$

We can introduce here the following notation:

$$\frac{dN_1}{dt} = \text{rate of increase of the number of prey.}$$

$b_1$  = coefficient of natural increase of prey (birth rate minus death rate).

$b_1N_1$  = natural increase of the number of prey at a given moment.

$f_1(N_1, N_2)$  = the function characterizing the consumption of prey by predators per unit of time. This is the greater the larger is the number of predators ( $N_2$ ) and the larger is the number of the prey themselves ( $N_1$ ).

$$\frac{dN_2}{dt} = \text{rate of increase of the number of predators.}$$

$F(N_1, N_2)$  = the function characterizing simultaneously the natality and the mortality of predators.

We can now translate the equations (20) into mathematical language by writing:

$$\left. \begin{aligned}
 \frac{dN_1}{dt} &= f_1N_1 - f_1(N_1N_2) \\
 \frac{dN_2}{dt} &= F(N_1, N_2)
 \end{aligned} \right\} \dots\dots\dots(21)$$

In a particular case investigated by Volterra in detail, the functions in these equations have been somewhat simplified. He put



$f_1(N_1, N_2) = k_1 N_2 N_1$ , e.g., the consumption of prey by predators is directly proportional to the product of their concentrations. Also  $F(N_1, N_2) = k_2 N_2 N_1 - d_2 N_2$ . Here  $k_2 N_2 N_1$  is the increase in the number of predators resulting from the devouring of the prey per unit of time, and  $d_2 N_2$  - number of predators dying per unit of time ( $d_2$  is the coefficient of mortality). This translation of (20) gives

$$\left. \begin{aligned} \frac{dN_1}{dt} &= b_1 N_1 - k_1 N_2 N_1 \\ \frac{dN_2}{dt} &= k_2 N_2 N_1 - d_2 N_2 \end{aligned} \right\} \dots\dots\dots(21a)$$

These equations have a very interesting property, namely the periodic solution, which has been discovered by both Lotka ('20) and Volterra ('26). As the number of predators increases the prey diminish in number,<sup>5</sup> but when the concentration of the latter becomes small, the predators owing to all insufficiency of food begin to decrease.<sup>6</sup> This produces an opportunity for growth of the prey, which again increases in number.

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<sup>5</sup> When the number of predators ( $N_2$ ) is considerable the number of the prey devoured per unit of time ( $k_1 N_1 N_2$ ) is greater than the natural increase of the prey during the same time ( $+b_1 N_1$ ), and ( $b_1 N_1 - k_1 N_1 N_2$ ) becomes a negative value.

<sup>6</sup> With a small number of prey ( $N_1$ ) the increase of the predators owing to the consumption of the prey ( $+k_2 N_1 N_2$ ) is smaller than the mortality of the predators ( $-dN_2$ ), and  $k_2 N_1 N_2 - dN_2$  becomes a negative value.

---

(2) In our discussion up to this point we have noted how the process of interaction between predators and prey can be expressed in a general form covering a great many special cases (equation 21), and how this general expression can be made more concrete by introducing certain simple assumptions (equation 21a). There is no doubt that we shall not obtain any real insight the nature of these processes by further abstract calculations, and the reader will have to wait for Chapter VI where the discussion is continued on the sound basis of experimental data.

Let us better devote the remainder of this chapter to two rather special problems of the natural increase of both predators and prey in a mixed culture simply in order to show how the biological reasoning can be translated into mathematical terms. In the general form the rate of increase in the number of individuals of the predatory species resulting

from the devouring of the prey  $\frac{dN_2}{dt}$  can be represented by means of a certain geometrical increase which is realized in proportion to the unutilized opportunity of growth. This unutilized opportunity is a function of the number of prey at a given moment:  $f(N_1)$ . Therefore,

$$\frac{dN_2}{dt} = b_2 N_2 f(N_1) \dots\dots\dots(22)$$

The simplest assumption would be that the geometric increase in the number of predators is realized in direct proportion to the number of prey ( $\lambda N_1$ ). Were our system a simple one we could say with Lotka and Volterra that the rate of growth might be directly connected with the number of encounters of the second species with the first. The number of these encounters is proportional to the number of individuals of the second species multiplied by the number of individuals of the first ( $\alpha N_1 N_2$ ), where  $\alpha$  is the coefficient of proportionality. If it were so, the increase of the number of predators would be in direct proportion to the number of the prey. Indeed, if the number of the prey  $N_1$  has doubled and is  $2N_1$ , the number of their encounters with the predators has also doubled, and instead of being  $\alpha N_1 N_2$  is equal to  $\alpha N_2 2N_1$ . Consequently the increase in the number of predators instead of the former  $b_2 N_2 \lambda N_1$  would become

equal to  $\frac{dN_2}{dt} = b_2 N_2 \lambda 2N_1$ , and the relative increase (per predator)

would be therefore:  $\frac{1}{N_2} \frac{dN_2}{dt} = b_2 \lambda 2N_1$ . In other words, the relative

increase  $\frac{1}{N_2} \frac{dN_2}{dt}$  would be a rectilinear function of the number of

prey  $N_1$ , i.e., with a rise of the concentration of the prey the corresponding values of the relative increase of the predators could be placed on a straight line ( $ab$  in Fig. 7). But experience shows the following: If we study the influence of the increase in the number of the prey per unit of volume upon the increase from one predator per unit of time, we will find that this increase rises at first rapidly and then slowly, approaching a certain fixed value. A further change in density of the prey does not call forth any rise in the increase per predator. In the limits which interest us we can express this relationship with the aid of a curve rapidly increasing at first and then approaching a certain asymptote. Such a curve is represented in Figure 7 ( $ac$ ). The concentration of prey ( $N_1$ ) is marked on the abscissae, and

the relative increase in the number of predators  $\left( \frac{1}{N_2} \frac{dN_2}{dt} \right)$ , or the rate of growth per predator at different densities of prey, is marked on the ordinates. The curve connecting the relative increase of the predators with the concentration of the prey can be expressed by the equation:  $y = a(1 - e^{-kx})$ ,<sup>7</sup> which in our case takes the following form:

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<sup>7</sup> This is the simplest expression of the curve of such a type, which is widely used in modern biophysics. It is deduced from the assumption that the rate of increase is proportional to still unutilized opportunity for increase taken in an absolute form: For experimental verification see Chapter VI.

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$$\frac{1}{N_2} \frac{dN_2}{dt} = b_2 (1 - e^{-\lambda M}) \dots\dots\dots(23)$$

The properties of this curve are such that as the prey becomes more concentrated the relative increase of the predators rises also, approaching gradually the greatest possible or potential increase  $b_2$  (see Fig. 7). The meaning of the equation (23) is that instead of the assumption of a linear alteration of the relative increase which was justified in the case of the competition for common food discussed before, we now take a further step and express a non-linear relation of the increase per predator with the concentration of the prey. All this will be easier to understand when in Chapter VI we pass on the analysis of the experimental material. We shall then explain also the meaning of the coefficient  $l$  in the equation (23).

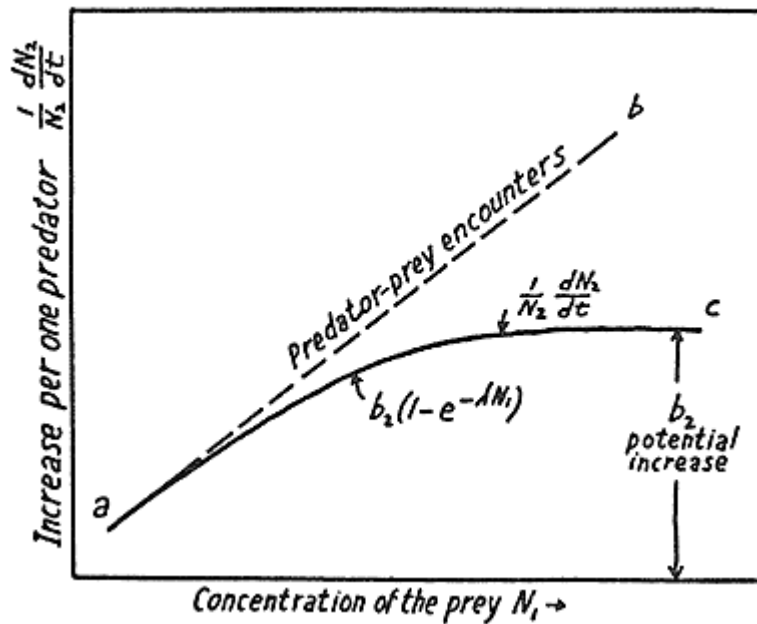


Fig. 7. The connection between the relative increase of the predators and concentration of the prey.

(3) The question now arises as to how to express the natural increase of the prey. As noticed already, the growth of the prey in a limited microcosm in the absence of predators can be expressed in the form of a potential geometric increase  $b_1 N_1$ , which at every moment of time is realized in dependence on the unutilized opportunity for growth  $\frac{K_1 - N_1}{K_1}$ . Therefore, the natural increase in the number of prey per unit of time can be expressed thus:

$$\frac{dN_1}{dt} = b_1 N_1 \frac{K_1 - N_1}{K_1} \dots\dots\dots(24)$$

It is easy to see that in the presence of the predator devouring the prey the expression of the unutilized opportunity for growth of the latter will take a more complex form. The unutilized opportunity for growth will, as before, be expressed by the difference (taken in a relative form) between the maximal number of places which is possible under given conditions ( $K_1$ ), and the number of places already occupied. But the number of prey ( $N_1$ ) which in the presence of the predator exist at the given moment, does not reflect the number of the "already occupied places." In fact the prey which have been devoured by the predator have together with the actually existing prey participated in the utilization of the environment, i.e., consumed the food and excreted waste products. Therefore, the degree of utilization of the

environment is determined by the total of the present population ( $N_1$ ) and that which has been devoured ( $n$ ).<sup>8</sup> The expression of the unutilized opportunity for growth of the prey will have then the following form:

$$\frac{K_1 - (N_1 + n)}{K_1} \dots\dots\dots(25)$$

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<sup>8</sup>These calculations are true only in the case of the competition for a certain limited amount of energy (see Chapter V). In other words it is assumed that the nutritive medium is not changed in the course of the experiment. With change of the medium at short intervals (as discussed in Chapter V) the term  $n$  disappears, and the situation becomes more simple.

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Here we arrive at a very interesting conclusion, namely, that *the development of a definite biological system is conditioned not only by its state at a given moment, but that the past history of the system exerts a powerful influence together with its present state*. This fact is apparently very widespread, and one can read about it in a general form in almost every manual of ecology. Lotka and Volterra expressed mathematically the role of this circumstance in the processes of the struggle for existence.

In order to complete the consideration we have to express the number of the devoured prey from the moment the predator is introduced up to the present time. If in every infinitesimal time interval the predator devours a certain definite number of prey then the total number of the devoured prey will be equal to the sum of the elementary quantities devoured from the moment the predator is introduced up to the given time ( $t$ ). This total can be apparently expressed by a definite integral.

(4) We cannot at present ignore the difficulties existing in the field of the mathematical investigation of the struggle for life. We began this chapter with comparatively simple equations dealing with an idealized situation. Then we had to introduce one complication after another, and finally arrived at rather complicated expressions. But we had in view populations of unicellular organisms with an immense number of individuals, a short duration of generations and a practically uniform rate of natality. The phenomena of competition are reduced here to their simplest. What enormous difficulties we shall, therefore, encounter in attempts to find rational expressions for the growth of more complicated systems.<sup>9</sup> Is it worth while, on the whole, to follow this direction of investigation any further?

<sup>9</sup>We can have an idea of this from the recent papers of Stanley ('32) and Bailey ('33) who try to formulate the equations of the struggle for existence for various insect populations.

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There is but one answer to this question. We have at present no other alternative than an analysis of the elementary processes of the struggle for life under very simple conditions. Nothing but a very active investigation will be able to decide in the future the problem *M* of the behavior of the complicated systems. Now we can only point out two principal conditions which must be realized in a mathematical investigation of the struggle for existence in order to avoid serious errors and the consequent disillusionment as to the very direction of work. These conditions are: (1) The equations of the growth of populations must be expressed in terms of the populations themselves, i.e., in terms of the number of individuals, or rather of the biomass, constituting a definite population. It must always be kept in mind that even in such a science as physical chemistry it is only *after* the course of chemical reactions has been quantitatively formulated in terms of the reactions themselves, that the attempt has been made to explain some of them on the ground of the kinetic theory of gases. (2) The quantitative expression of the growth of population must go hand in hand with a direct study of the factors which control growth. Only in those cases, where the results deduced from equations *are confirmed by the data obtained through entirely different methods, by a direct study of the factors limiting growth*, can we be sure of the correctness of the quantitative theories.

